Grizzly Bear Population and Density Estimates for the 2006 Alberta Unit 5 Management Area Inventory

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The work and results of this project were a collaborative effort of specialists in various aspects of wildlife biology, statistics, and genetics. The role of each member is as follows:

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1. Abstract

As part of ongoing grizzly bear management efforts in Alberta the Department of Sustainable Resource Development has been conducting population estimates in bear management units (BMA's) along the eastern slopes of Alberta. This work is focused on establishing current population status and spatial distribution of grizzly bears in these BMA's. This report provides grizzly bear population and density estimates for a study area that includes the Alberta Provincial grizzly bear management area 5 (BMA 5), Kananaskis and Peter Lougheed Provincial Parks, and a part of Banff National Park. In 2006, a DNA hair capture grid (7639 km^2) was sampled. One hundred and sixty 7x7 km grid cells were sampled with 1 hair capture site for 4 sampling sessions. Of these, nineteen 7x7 cells were located wholly within Banff Park to assist with population closure. In addition, 8 transect cells were sampled in plains areas in the southeast to detect occupancy of bears in these areas (but were not used in the mark-recapture analysis). Each hair capture site was moved between sessions to ensure adequate coverage of cell areas for cells within the main sampling grid. Eighty five individual bears were captured at sites on the main sampling grid. The distribution of bears was clumped along the west side of the study area. Data-based tests and GPS collared bears showed that the population was not geographically closed with 67.6% of VHF or GPS collared bears locations occurring on the sampling grid. The estimate of the superpopulation of bears (bears including dependent offspring, within the sampling grid and surrounding area during the time that sampling was conducted) was 133 (SE=18.12, CI=109 to 183). The average number of bears on the sampling grid was estimated by multiplying the superpopulation number by the proportion of GPS/VHF collared bear locations on the sampling grid (0.676) to estimate an average number of bears on the sampling grid at any one time of 89.9 (SE=15.73 CI=75 to 116). The average number of bears at any one time was divided by the sampling grid area (7639 km^2) to derive a density estimate of 11.77 bears per 1000 km^2 (SE=2.06 CI=9.9 to 15.2) on the sampling grid. We recommend that for management purposes the estimate of the average number of bears on the sampling grid area (89.9) be used.

2. Introduction

As part of ongoing grizzly bear management efforts in Alberta the Department of Sustainable Resource Development has been conducting population estimates in bear management units (BMA's) along the eastern slopes of Alberta since 2004. In 2003 a detailed analysis of genetic samples from grizzly bears, collected over a 22-year period, was conducted to delineate genetically distinct population units (Proctor and Paetkau 2004). This analysis showed that previous population unit boundaries (BMA's) did not fully match genetic population units and therefore recommendations were made to modify the management unit boundaries at that time.

While this BMA review was in progress, attention was focused on the status and management of grizzly bears in Alberta. This resulted in recognition that adequate

population data was needed to improve management capabilities and a greater understanding of current grizzly bear population status. In 2004 and 2005 inventory projects were conducted in management units 3 and 4 resulting in population and density estimates for these areas (Boulanger et al. 2005a, Boulanger et al. 2005b, Boulanger et al. 2006).

This report provides a population estimate for the Alberta provincial grizzly bear DNA mark-recapture inventory project that occurred in 2006 on a study area containing Alberta grizzly bear management area 5 (including protected areas) and a portion of Banff National Park (BNP). From an inventory perspective, the study area attempted to contain most of this biological unit (between Highways 1 and 3) to minimize violation of population closure, while surveying an entire biologically-based management unit. Appendix 1 displays Unit 5 in relation to other bear management units in Alberta.

3. Methods

3.1. Field methods

A systematic DNA sampling grid of 7x7 km grid cells was placed within the project study area boundary (Figure 1). Because population closure is an important assumption of our population estimators, we used data from previous population genetic analyses (Proctor and Paetkau 2004) to design the study area to minimize the movement of bears across the boundaries. Our study area encompassed most of grizzly bear management area 5 which was bounded by Highways 1 and 3 providing relative closure to the south and north respectively (Proctor and Paetkau 2004, Proctor et al. 2005). To the east, the area extended into land (minimally occupied or) unoccupied by grizzly bears. Here we additionally sampled 8 transect cells (with sites not moved between sessions) to determine bear occupancy in these areas. The western edge was defined by the British Columbia border that also formed the height of land therefore maximizing population closure. Some cells were partially bisected by the continental divide. Sites were placed in these cells in proportion to the area of the cell that was within the sampling grid. This resulted in 160 cells being sampled with 12 additional cells that were partially sampled. Seven transect cells were sampled off the western side of the grid to help assess closure violation on this side of the grid. One potential issue with sampling the northwest border of bear management area 5 was that it was not topographically closed to bear movement in and out of Banff National Park. Therefore, we adjusted the northwest border of the grid to sample 19 cells wholly within BNP therefore making Highway 1 and 93 to the B.C. border the northern boundary. We knew from previous research (Gibeau 2000, Herrero 2005) that Highway 1 was a significant barrier to bear movement and felt that Highway 93 was at least a partial barrier to bear movement therefore accommodated the assumption of population closure as much as possible. Using the height of land as the western boundary and Highway 1 as the northern boundary we estimated the sampling area to be 7639 km^2 (Figure 1).

One hair capture site was placed in each grid cell for 4, 14 day sampling sessions in the spring and early summer of 2006. Site selection was done prior to fieldwork and was based upon grizzly bear RSF models (Nielsen et al. 2002, Nielsen et al. 2006), GPS collar locations, remote sensing-based habitat mapping (McDermid 2005), aerial photographs, and expert opinion of bear biologists. Each hair capture site was moved after each session to ensure equal coverage of each cell. One strand of barbed wire at each site was used for sampling bear hair. Previous research as part of the 2004 Alberta 3B4B Inventory project (Boulanger et al. 2006) suggested that a design with sites moved and one strand of barbed wire was optimal for mark-recapture sampling.

At each hair capture site, a strand of barb wire approximately 50 cm off the ground was attached around 3 to 6 trees to catch the hair of bears investigating the site. A scent lure mixture of 2 litres of rancid cow blood and 1 litre of rancid fish liquid was poured on top of a pile of wood debris and moss in the middle of the barb wire enclosure to attract bears without providing them a food reward (Woods et al. 1999). Grizzly bear hair was collected from each hair capture site. Applicable samples were then genotyped (Paetkau 2003). See Appendix 2 for details on the minimization of genetic error rates.

Figure 1: DNA sampling grid layout for the Alberta 2006 DNA mark-recapture population inventory project. Each cell was 49 km^2. Main sampling grid cells had 1 hair capture site that was moved for each of 4 sampling sessions.

3.2. Data summary

Data was summarized in terms of capture frequencies for individual bears. For traditional mark-recapture analysis, multiple captures of an individual within one session are pooled into one capture per session. Summary statistics were generated for the pooled data set. See Appendix 3 for background information on mark-recapture population estimation.

3.3. Assessment of closure violation

In review, closure violation is caused by bears moving in and out of the study areas during sampling (White et al. 1982). If closure violation is occurring, mark-recapture population estimates will pertain to the "superpopulation" of bears in the *sampling grid and surrounding area during the time that sampling was conducted* (White 1996, Kendall 1999). For estimation of density and comparison of different areas, the average number of bears on the sampling grid at any one time is most applicable. For this reason, we used data-based tests for closure violation (Boulanger and McLellan 2001), and used data from GPS and VHF collared bears to scale superpopulation estimates into average population size estimates (White and Shenk 2001) as discussed later.

The Pradel (1996) model in program MARK (White and Burnham 1999) was used to assess the data set for closure violation (Boulanger and McLellan 2001). The main premise for this test is that, if closure violation was occurring, grizzly bears that were near the grid edge ("edge" grizzly bears) would have lower recapture rates due to a reduced trap encounter rate compared to grizzly bears farther from the edge ("core" grizzly bears). In addition, if grizzly bears moved from the grid for the entire sampling period, then edge grizzly bears would exhibit a lower apparent survival estimate than core grizzly bears. Also, grizzly bears, which immigrated into the grid area during sampling, would be more prone to be captured near the grid edge. The distance from edge of capture location was considered the shortest distance from the grid edge to the mean location of hair capture sites where a grizzly bear was identified during the entire project. The Pradel (1996) model estimates apparent survival (ϕ), recruitment (f) and recapture probability (p). The estimates for recapture rate are for the exact sampling period, whereas the estimates for the apparent survival rate (ϕ) and recruitment (f) correspond to the interval before the given sampling period.

We assumed that the population of grizzly bears was demographically closed for this analysis. The duration of sampling was <2 months so this assumption was considered reasonable. Apparent survival equals true survival (S) (due to mortality) times the fidelity of grizzly bears (F) to the sampling grid (ϕ=SF). Because the population was demographically closed, we assumed that true survival equalled one (S=1) and therefore relative changes in ϕ reflect grizzly bear fidelity to the sampling grid rather than actual mortalities, i.e., (ϕ=F). The Pradel recruitment rate estimates the number of new individuals in the population at time j+1 per individual at time j. We know that the

number of births during sampling was minimal and therefore measures of recruitment reflected permanent immigration or "additions" of grizzly bears into the sampling grid. For the sake of simplicity we will refer to ϕ as the rate of "Fidelity" and f as the rate of "Additions" in the rest of this report.

As an initial appraisal of population closure we evaluated the goodness of fit of Pradel models constrained to only allow certain forms of closure violation as first proposed by (Stanley and Burnham 1999). The exact models used in the test of Stanley and Burnham (1999) were the fully open Jolly Seber model (JS), a recruitment but not mortality model (NM), a mortality but not recruitment model (NR), and a closed model with no mortality or recruitment (M_t). We emulated the approach of Stanley and Burnham (1999) by fixing parameters to appropriately constrain the Pradel model (Boulanger and McLellan 2001).

We then used continuous covariates to model the relationship of distance from edge for ϕ, f, or p as a logistic function. The potential shapes that the logistic curve, which is used to model covariates in MARK, could accommodate was restrictive, and therefore logistic equations with log transformed (+1) (Zar 1996) distance from edge and higher order polynomial (i.e. dfe^2 log $(dfe)^2+1$) distance from edge terms were also considered. Covariates were standardized in program MARK by the mean and standard deviation of observed distances (White et al. 2002). A logit link was used for all analyses.

In addition to covariates, both sex and time specific model formulations were considered in the building of mark-recapture models. The fit of models was evaluated using the Akaike Information Criterion (AIC) index of model fit. The model with the lowest AICc score was considered the most parsimonious, thus minimizing estimate bias and optimizing precision (Burnham and Anderson 1998). The difference in AICc values between the most supported model and other models (ΔAICc) was also used to evaluate the fit of models when their AICc scores were close. In general, any model with a ΔAICc score of less than 2 was worthy of consideration.

An assumption of the Pradel analysis was that capture, survival, and movements are independent. In addition, it is assumed that all individuals within a group have similar apparent survival rates and similar values of other model parameters. If individuals are not independent, the multinomial variances from the models become inflated or overdispersed, which causes underestimation of parameter variances and overfitting of models. Various goodness-of-fit tests are available to test and estimate the degree of overdispersion in the data set. Because lack of fit in the Pradel models can only be assessed for the recapture portion of the encounter history, the goodness-of-fit test in Program RELEASE (Burnham et al. 1987) was used to assess goodness-of-fit. If overdispersion was detected (as indicated by $\hat{c} > 1$), we used $QAIC_c$ instead of AIC_c model selection criterion to select optimal models (Burnham and Anderson 1998, White et al. 2002).

3.4. Analysis of effect of previous live capture history on capture probabilities

One potential issue with this study was that a large population of bears in the study area were previously live captured and radio collared as part of research and management activities. Some bear biologists have suggested that this could lower the capture probabilities of these bears or make these bears "uncatchable". Lower capture probabilities of radio collared bears will not bias estimates if heterogeneity models are used for estimation. However, if a segment of the population is "uncatchable" (capture probability=0) then it is invisible to DNA sampling potentially resulting in negatively biased population estimates. One problem with exploring this issue is that it is impossible to tell if a previously collared bear that was not detected in DNA sampling was still on the sampling grid or alive. We used a recently developed method that utilizes both detected and historically collared bears to estimate the DNA-based capture probabilities of currently and previously collared bears. This method has been applied to the previous 2004-2005 DNA data sets (Boulanger et al. 2007).

We applied occupancy models (MacKenzie et al. 2002) to estimate the probability of capture for DNA and radio collared bears (p) and the probability that radio collared bears were on the sampling grid during the time of DNA sampling (Ψ). Occupancy models estimate detection probability in an analogous fashion to closed population size estimation models except that occupancy of the sample unit (sites in most cases, bears in our study) is estimated rather than the population size of sample units (MacKenzie et al. 2002, MacKenzie et al. 2004). A key distinction between occupancy and closed N models is that undetected sample units (i.e. 0000 encounter histories) are included in the encounter history for occupancy models whereas closed models only use sample units that are detected at least once. Therefore, occupancy models have higher power to detect differences in capture probabilities of collared bears since they also consider collared bears that were not detected on the grid but were known to be on the grid during the year of the survey or previous years.

We framed our question with bears as the sample unit of interest, and whether a DNA sampling grid was occupied by individual bears that previously had been live captured and known to be alive on the grid area, although possibly not present currently. The capture histories from the 2006 DNA surveys were used to model detection and occupancy rates of bears. Bears that had been previously monitored on the area but were not detected in DNA projects received a 0000 capture history. Bears were divided into groups based on the year last monitored, i.e., years since the bear was last known to be alive (via telemetry or sightings) and on the DNA survey grids. Bears that were currently being monitored (using VHF radio telemetry or GPS methods) or bears captured in DNA hair snags were both assigned into the 0 years since last monitored group. Previously live captured bears were assigned to a group according to the year they were last monitored up to 12 years previous. This categorization resulted in 13 unique groups in the MARK occupancy model analysis. We first constrained Ψ to have no within-year (occasion-based) variation, meaning that the bear population was demographically and

geographically closed during the DNA survey. We then used the design matrix in MARK (White et al. 2002) and a log-link (e^{β}) to model estimates of Ψ as an exponentially decreasing function for each group in the analysis. This model allowed us to estimate the occupancy probability of bears that we did not know whether they still existed on the DNA survey grids. The bears in the 0 group were given a 0 in the design matrix. This process resulted in a $\beta \times 0$ term of 0 and resulting estimate of $\Psi = 1$ since $e^0 = 1$ because occupancy of these bears on the grid was certain. Other groups were constrained successively with design matrix values 1 to 12 which modelled an exponential decline in the estimated Ψ, and thus the apparent survival rate of bears with unknown occupancy status.

We introduced models into the analysis with capture probabilities that were sex specific and varied as a function of whether bears were previously or currently collared. We also considered interactions between sex and previous collaring history. As with the Pradel analysis, AICc model selection was used to select models that were most supported by the data.

3.5. Closed population estimation model selection

We primarily used the Huggins closed models (Huggins 1991) in program MARK for estimation model selection. Sexes of grizzly bear were entered as groups in this analysis, testing whether sexes displayed differing forms of capture probability variation. Models with time, heterogeneity, and behaviour variation were considered in the analysis. Mixture model heterogeneity estimators (Pledger 2000) as incorporated in program MARK (White and Burnham 1999) were used to model heterogeneity variation. This is modeled by letting capture probabilities come from more than one capture probability distribution. There are three parameters with the 2-distribution mixture model. The parameters are the probability that a given capture probability will come from the first distribution (π), the mean capture probability of the first distribution (θ_1), and the mean capture probability of the second distribution (θ_2). The probability that the capture probability comes from the second distribution is $1 - \pi$ (Pledger 2000). As with the Pradel analysis, AICc model selection was used to assess parsimonious estimation models. In addition, tests for specific forms of capture probability variation in program CAPTURE (Otis et al. 1978) were used to assess capture probability variation and compared with MARK model selection results.

3.6. Simulation tests of estimators

The optimal model and associated estimator for a mark-recapture data set is dependent on the population size of bears on the sampling grid, capture probability of bears in the population, and forms of capture probability variation in the data set. The best way to determine optimal models and associated estimators is through data-based model selection (discussed in Section 3.5) and simulation methods (Boulanger et al. 2004). Two simulation methods were used to test estimation models. First, results from past projects,

radio collared studies of grizzly bears, and expert opinion were used to devise simulation models of likely forms of capture probability variation in the bear population. These models were used to evaluate the precision of estimators across a range of sampling parameters. Second, direct estimates of capture probability variation obtained in program MARK were used to parameterize data-based simulations.

As summarized in Table 1, each of these approaches has strengths and weaknesses. Simulation models based on data-based simulations are limited to detectable forms of capture probability variation in mark-recapture data sets. Because most data sets are sparse it is probable that certain forms of heterogeneity variation, such as low capture probabilities of cubs of the year, are not detected. Therefore, telemetry and expert based simulations are useful to allow exploration of non-detected forms of capture probability variation.

Table 1: Methods used to estimate precision and evaluate estimator performance.

Evaluation method	Strengths	Weaknesses
1) Simulations based on expert opinion and telemetry estimates of cub capture probability	Incorporates biologically-based forms of capture probability variation that may be difficult to detect in field data	Makes "expert" assumptions about main forms of capture probability variation in data that cannot be directly tested.
2) Data-based simulations	Uses direct estimates of variation from data with minimal "expert-based" assumptions	May not include forms of capture probability variation not detected due to sparse data

Each of these methodologies are explained in detail in Appendix 4.

Estimators were evaluated in terms of bias, precision, and confidence interval coverage. Bias was defined by percent relative bias

$$\text{P.R.B.} = \frac{(\hat{N} - N)}{N}$$ where $\hat{N}$ is the estimate population size from each model and N was the true number of bears in the simulation. The optimal level of precision was indexed by the coefficient of variation (CV) that is

$$CV(\hat{N}) = {SE(\hat{N})}/{\hat{N}} \; X \; 100$$

The CV is a convenient way to compare precision of different projects since it expresses standard error in percentage units of the estimate. The confidence interval width is approximately ± 1.96 (CV). So if a project has a CV of 10% then the confidence interval is roughly ± 20% of the estimated population size. Confidence intervals for mark-recapture project are seldom symmetrical so this is a rough approximation. Confidence

intervals can be conceptualized as a bell shaped curve with the most probable estimate being the point estimate and the least probable estimates being on either end of the confidence interval. Bias and precision were considered simultaneously by the mean squared error (M.S.E.), which is the absolute value of percent relative bias plus the coefficient of variation. An estimator with the lowest M.S.E. displays the best balance between bias and precision. In addition, confidence interval coverage was considered, which was the proportion of time the estimated population size bracketed the true population value.

3.7. Population estimates

Population estimates from the program MARK models and program CAPTURE models were considered. Estimates from all of the Huggins MARK models were model-averaged, allowing population estimates that were influenced by all the estimation models considered in the analysis. Optimal estimation models were chosen based upon the results of model selection and simulations.

3.8. Average population size on study area grid and density estimates

A relatively large number of bears have been radio collared in the Unit 5 area as part of the East Slopes (Herrero 2005), Kananaskis (Jon Jorgenson, Sustainable Resource Development, Fish and Wildlife Division, Canmore, unpublished data), and Foothills Model Forest (Stenhouse and Graham 2005) grizzly bear research projects. We therefore used the movement of these bears to estimate the degree of closure violation. First, we defined the sample of radio-collared bears on the sampling grid by determining what bears had at least 1 location on the sampling grid during the time it was collared. We then estimated the proportion of locations on the DNA mark-recapture grid for each bear and year combination. Data was subsetted for the interval in which DNA sampling occurred (May 24 to July 24). Any bear-year combination that had at least 20 locations was considered in the estimation. We then took the mean proportion of locations on the grid for each bear (given that some bears were collared multiple years) across multiple years. One potential issue with the analysis was that the proportion of males and females collared bears was not the same as the proportion of males and females in the population. Since males move more it was likely that they violated closure to a greater degree than females. We corrected for this by weighting the contribution of each bear in the analysis by the proportion of its sex in the population. The proportion of each sex in the population was estimated from sex-specific DNA mark-recapture population estimates. Using these weights, the mean proportion of locations on the grid was then estimated as the weighted mean (Zar 1996) of all the bears in the analysis. This approach avoided psuedoreplication by maintaining individual bears as the sample unit. Superpopulation estimates were then multiplied by this proportion to estimate the average number of bears on the study area at one time. Both the CAPTURE and MARK superpopulation estimate and the proportion of radio marked bears on the grid estimate have error. Therefore, we used the delta method (Seber 1982) to estimate combined variances under the assumption that correlation between population estimates and the proportion of time on the grid was

zero. We calculated log-based confidence-intervals for the average number of bears on the sampling grid estimates (White and Shenk 2001).

4. Results

4.1. Data summary

Eighty five bears (40 males and 45 females) were identified with the sampling grid hair capture sites of which five were also captured at transect sites on the western side of the sampling grid. Sixteen additional bears were also identified in transect sites on the western side of the sampling grid. Seven bears were captured within the DNA grid that were recaptured from a 1997 DNA survey conducted in adjacent lands within British Columbia. No bears were captured in transect cells on the eastern side of the sampling grid. The distribution of captures was clumped in the western mountainous regions with less captures on the eastern plains area (Figure 2).

Figure 2: Distribution of captures at hair capture sites for the Alberta Unit 5 inventory projects Sites are scaled by the number of unique bear captures that occurred at the site over the course of the project.

Mean capture locations of DNA bears also suggest that most bears were found on the western edge of the study area (Figure 3). Sexes were intermixed fairly evenly through the main areas of capture.

Figure 3: Mean capture locations for individual bears in the Alberta Unit 5 inventory project.

Summary statistics for mark-recapture modeling suggest that there was minimal temporal variation in capture rates with the most captures occurring during session 3 (Table 2). The number of newly caught (genotyped) individuals decreased with session for both sexes suggesting that sampling was effective in capturing the majority of bears in the area. However, compared to projects conducted in 2004 and 2005, more new bears were captured in session 4 suggesting that we caught a smaller proportion of the total population than we did in previous years. Most bears were captured once or twice with few bears being captured 3 or 4 times.

Table 2: Summary statistics for the Alberta Unit 5 Inventory DNA data set.

Statistic	Session				
	1	2	3	4	total
males					
Animals caught n(j)	16	13	18	13	
Total individuals caught M(j)	0	16	24	34	40
Newly caught u(j)	16	8	10	6	
Frequencies f(j)	25	11	3	1	
females					
Animals caught n(j)	14	17	22	21	
Total individuals caught M(j)	0	14	27	39	45
Newly caught u(j)	14	13	12	6	
Frequencies f(j)	24	14	6	1	
Pooled					
Animals caught n(j)	30	30	40	34	
Total individuals caught M(j)	0	30	51	73	85
Newly caught u(j)	30	21	22	12	
Frequencies f(j)	49	25	9	2	

4.2. Tests for closure violation

The Program RELEASE goodness-of-fit test for model ϕ(sex x time) p(sex x time) suggested minimal overdispersion of multinomial likelihoods or $\hat{c} = 1$ ($\chi^2 = 6.5$, df=8, p=0.59) and therefore AICc was used for model selection. Pradel model selection results suggested that grid fidelity was relatively high as indicated by support of models with ϕ (apparent survival) fixed at 1 (implying no movement off grid during sampling). Model selection results suggested that movement onto the sampling grid did occur as indicated by support of models with f varying as a function of mean capture from grid edge (Table 3).

Table 3: Pradel model selection. Akaike Information Criteria (AIC_c), the difference in AIC_c values between the *i*th model and the model with the lowest AIC_c value (ΔAIC_c), Akaike weights (w_i), and number of parameters (K) are presented

Model	AICc	ΔAICc	w_i	K	Deviance
ϕ(1) p(.) f(ld+ld^2)^{A,B}	419.8	0.00	0.517	4	411.5
ϕ(1) p(sex) f(ld+ld^2)	421.4	1.67	0.225	5	411.0
ϕ(1) p(sex+F(T))^C f(ld+ld^2)	421.9	2.14	0.177	6	409.3
ϕ(1) p(.) f(0)	425.0	5.19	0.039	1	422.9
ϕ(sex) p(sex+F(T)) f((ld+ld^2)	426.4	6.63	0.019	8	409.3
ϕ(.) p(.) f(.)	428.0	8.25	0.008	3	421.8
ϕ(.) p(sex) f(.)	429.2	9.43	0.005	4	420.9
ϕ(sex) p(sex+F(T)) f(sex(+d+ld^2)	429.4	9.58	0.004	9	409.9
ϕ(sex+ld p(sex+F(T) f(sex+ld)	430.2	10.40	0.003	9	410.7
ϕ(ld) p(.) f(ld)	430.7	10.91	0.002	5	420.2
ϕ(ld+ld2) p(.) f((ld+ld^2)	432.9	13.16	0.001	7	418.0
ϕ(sex) p(sex) f(sex)	433.0	13.26	0.001	6	420.4
ϕ(sex*t) p(sex*t) f(sex*t)	462.6	42.82	0.000	20	415.2

[A] 1 or 0 denotes that ϕ or f was fixed at 1 or 0 (implying complete closure).
[B] ld denotes that the log of the distance of mean capture of bear from grid edge
[C] F(T) denotes a linear trend in female capture probabilities.

Model averaged estimates of demographic parameters suggested that apparent survival rates were close to 1 implying there was minimal emigration from the sampling grid. Rates of addition were slightly above 0 suggesting some potential movement of bears into the sampling grid (Table 4).

Table 4: Model averaged estimates of Pradel model parameters

Parm	Sex	Estimate	SE	LCI	UCI
ϕ (emigration)	Male	0.99	0.06	0.87	1.00
	Female	1.00	0.01	0.99	1.00
f (immigration)	Male	0.02	0.08	0.00	0.92
	Female	0.02	0.04	0.00	0.78

One issue with model-averaged estimates is that they do not include models that have individual covariates such as distance of mean bear capture location from the edge of the sampling grid. The estimate of rates of addition from the most supported model (ϕ(1) p(.) f (ld+ld^2)) for the mean distance from edge of bears on the sampling grid (6.85 km) is 0.96 bears at session t+1 per bear at session t (SE=0.71, CI=0 to 1.88). This suggests that some of the bears captured at moderate mean distances (i.e., 6.85 km) from edge were potentially immigrant bears.

4.3. Occupancy model analysis of effect of previous collaring on capture

Forty four bears were collared and monitored previous to the 2006 DNA project that had at least 1 location on the sampling grid and therefore were potentially vulnerable to DNA capture. An additional 6 bears were monitored during the DNA project (Table 5). Of the six bears monitored on the grid, 4 were captured in DNA sites. Eight bears that were collared previous to 2006 were also captured. The other bears were not captured in DNA efforts. However, many of the bears from previous years were not residents as shown by the lower mean proportion of locations on the grid. So it is possible that these bears were still alive but not on the sampling grid. The estimate of occupancy is the probability that these bears were still on the grid in 2006. Occupancy models assume three potential fates for these bears; they were either killed or not on the sampling grid during DNA sampling (as reflected in estimates of occupancy), or on the sampling grid but not captured (as reflected in estimates of capture probability).

Table 5: The number of bears radio collared (and DNA captured) as a function of last year that they were monitored or sighted on the sampling grid. Also given is the proportion of locations on the sampling grid as an estimate of residency for bears last monitored in a given year. The mean number of points is the number of points used for estimates of residency. Estimates of residency from less than 20 points should be interpreted cautiously.

Year last monitored	Radio collared Bears		Proportion locations on grid	
	Total bears	DNA Captured	Mean	Mean points[A]
2006	6	4	0.99	16.0
2005	2	0	0.79	41.3
2004	8	3	0.73	122.1
2003	11	5	0.74	13.1
2002	7	0	0.63	105.4
2001	3	0	0.51	60.4
2000	1	0	0.40	5.8
1999	2	0	1.00	24.8
1998	1	0	0.18	5.8
1997	1	0	0.06	11.3
1996	2	0	0.95	3.3
1995	1	0	0.91	10.0
1994	5	0	0.58	9.5

[A]The mean number of telemetry points per year for bears to estimate proportion on grid.

Model selection results suggested that female bears that were collared or were previously collared had different capture probabilities than other bears (Table 6: Model 1). Also supported was a model with capture probabilities different for DNA and collared bears (Model 2), a model (Model 3) with equal capture probabilities for all bears, and a model with different capture probabilities for sex of bear and females that had been collared previously (model 4).

Table 6: Occupancy model selection. Akaike Information Criteria (AIC_c), the difference in AIC_c values between the *i*th model and the model with the lowest AIC_c value (ΔAIC_c), Akaike weights (w_i), and number of parameters (K) are presented. Yrmon is the years since a bear was last known to be alive on the sampling grid.

No	Model	AICc	ΔAICc	w_i	K	Deviance
1	p(res(F) ψ(yrmon)	499.8	0.00	0.188	3	493.6
2	p(res) ψ(yrmon)	500.3	0.45	0.150	3	494.1
3	p(.) ψ(yrmon)	500.4	0.57	0.141	2	496.3
4	p(sex+res(F) ψ(yrmon)	501.1	1.27	0.100	4	492.8
5	p(res+res(F)) ψ(yrmon)	501.8	1.97	0.070	4	493.5
6	p(.) ψ(yrmon+yrmon^2)	502.0	2.16	0.064	3	495.8
7	p(sex+res) ψ(yrmon)	502.2	2.32	0.059	4	493.8
8	p(sex) ψ(yrmon)	502.3	2.48	0.054	3	496.1
9	p(res(M)) ψ(yrmon)	502.5	2.62	0.051	3	496.3
10	p(sex+sex*res) ψ(yrmon)	503.2	3.41	0.034	5	492.7
11	π(.) $\theta_{1\&2}$(res(F) ψ(yrmon)	504.2	4.31	0.022	5	493.6
12	p(sex+res(M)) ψ(yrmon)	504.4	4.61	0.019	4	496.1
13	π(.) $\theta_{1\&2}$(+res) ψ(yrmon)	504.6	4.76	0.017	5	494.1
14	π(.) $\theta_{1\&2}$(.) ψ(yrmon)	504.7	4.81	0.017	4	496.3
15	π(.) $\theta_{1\&2}$(+res+sex) ψ(yrmon)	506.5	6.71	0.007	6	493.8

[A]res(F) refers to the capture probability for females that were previously or currently collared
[B]Models with π and $\theta_{1\&2}$ parameters are heterogeneity 2-point mixture models that are analogous to the Huggins closed M_{h2} mixture models described in Section 3.5.

Plots of capture probabilities for female bears from model 1 (Figure 4a) suggest that bears that were previously collared did have reduced capture probabilities, however, confidence intervals overlapped bears that were DNA captured only. In addition, confidence intervals were well above 0 suggesting that these bears had a non-zero capture probability, therefore minimizing bias in population estimates from heterogeneity models and estimators. Plots of probability of occupancy suggest that the probability of a bear being on the grid alive declined for bears collared in previous years (Figure 4b). As discussed later, this is probably due to many of the bears that were collared on the grid being partial residents (as indexed by proportion of radio locations on the sampling grid (Table 5)). In contrast, decline in occupancy probability was less rapid for the 2004-2005 grids that exhibited a higher degree of closure (as discussed later).

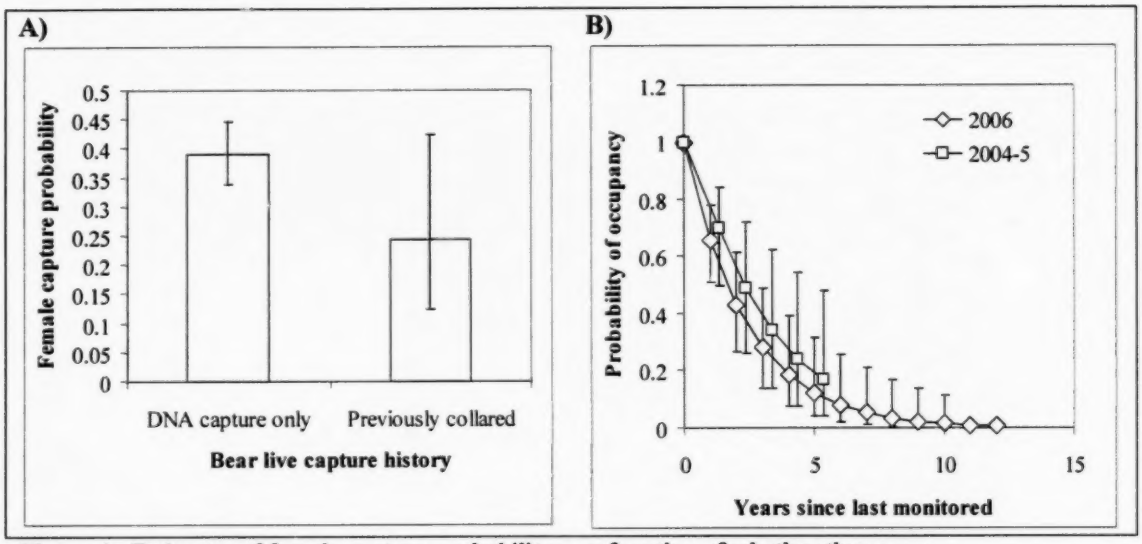

Figure 4: Estimates of female capture probability as a function of whether they were previously collared (A) and probability of bear occupancy on DNA grid as a function of year since last monitored (B). Estimates are given for the 2006 DNA project and 2004-5 project (from Boulanger et al. 2007) for comparison. No difference was detected between male capture probabilities from collared or DNA captured bears.

4.4. Population estimation model selection

Huggins model selection suggested that heterogeneity of capture probabilities existed in the data set as indicated by support of models capture probability varying by sex and whether a bear was collared as well as distance from mean capture from grid edge (Table 7). A model with undefined heterogeneity was also supported. A model that had a negative linear trend in capture probabilities (T(F) term) was also supported in addition to heterogeneity variation. Many models were supported by the data set (as indicated by ΔAICc values <2.0) that was probably due to lower capture probabilities of bears and subsequent lower power of model selection procedures.

Table 7: MARK Huggins closed model AICc model selection. Akaike Information Criteria (AIC_c), the difference in AIC_c values between the *i*th model and the model with the lowest AIC_c value (ΔAIC_c), Akaike weights (w_i), and number of parameters (K) are presented

Model	AICc	ΔAICc	w_i	K	Deviance
M_{th} p(sex+T(F)) [A]	425.4	0.00	0.140	3	419.3
M_{th2} π (.) $\theta_{1\&2}$ (+T(F))	425.6	0.22	0.125	4	417.5
M_h p(sex)	426.1	0.69	0.099	2	422.1
M_{th2} π (.) $\theta_{1\&2}$(+t3)	426.7	1.29	0.073	4	418.6
M_h p(sex)+ld [B]	427.0	1.56	0.064	3	420.9
M_{h2} π (.) $\theta_{1\&2}$(.)	427.1	1.66	0.061	3	421.0
M_{th2} π (.) $\theta_{1\&2}$(*T)	427.1	1.68	0.060	5	416.9
M_{th} p(sex+T)	427.1	1.70	0.060	3	421.0
M_{th} p(sex*T)	427.4	1.98	0.052	4	419.3
M_{th2} π(.) $\theta_{1\&2}$(+T(F)+resbear [C]	427.6	2.18	0.047	5	417.4
M_{th2} π(.) $\theta_{1\&2}$(sex+T(F))	427.6	2.19	0.047	5	417.4
M_{h2} π(.) $\theta_{1\&2}$(+T)	428.0	2.64	0.037	4	419.9
M_h p(sex+resbear)	428.1	2.73	0.036	3	422.1
M_t p(t)	428.2	2.84	0.034	4	420.1
M_{h2} π(.) $\theta_{1\&2}$(sex)	428.3	2.94	0.032	4	420.2
M_{h2} π(.) $\theta_{1\&2}$(+t)	430.3	4.94	0.012	6	418.1
M_{h2} π(.) $\theta_{1\&2}$(*sex)	430.4	5.00	0.011	5	420.2
M_{th} p(sex+t)	431.5	6.09	0.007	6	419.2

[A] T(F) denotes that a linear trend in capture probabilities was modelled for females
[B] ld denotes that the log of the distance of mean capture of bear from grid edge
[C] Resbear denotes capture probabilities as a function of whether a bear was previously collared.

4.5. Simulation tests of mark-recapture model estimators

A key question was whether heterogeneity (M_h) model estimators were robust to the levels of time variation observed in the data set. In addition, it was of interest whether lower capture probability levels in the data set influenced the MARK model selection method. Results suggested that most estimators showed reasonable bias levels with the exception of the M_t (Chao) and MARK model averaged estimates in the data-based and expert based simulations (Table 8). The poor performance of the MARK estimators was due to instability of the recently modified Huggins-Pledger estimator (Gary White, Colorado State University, Per. Comm.) Of the CAPTURE estimators, the M_h (Chao) estimator displayed the best performance with low mean squared error and confidence interval coverage close to 95% in all simulations. This results is not surprising given that the M_h (Chao) estimator performs best for data with lower capture probabilities (that cause other estimators such as the M_h (jackknife) to be negatively biased) (Chao 1989). Based on data-based model selection (that detected heterogeneity variation (Table 7) and these simulations we conclude the M_h (Chao) estimator was most suitable for this data set.

Table 8: Simulation results from data and expert based simulations.

Estimation model	PRB	CV	MSE	C.I. Coverage
Data-based simulations				
M_h (Chao)	-0.78	13.5	14.3	94.7
M_h (jackknife)	5.10	10.2	15.3	84.2
M_t (Chao)	-10.78	11.2	22.0	82.8
M_{th}	3.50	15.8	19.3	93.0
MARK Model ave	-17.41	37.6	55.0	51.2
Expert based simulations				
M_h (Chao)	2.23	15.5	17.8	94.8
M_h (jackknife)	6.16	10.2	16.4	84.6
M_t (Chao)	-9.75	12.8	22.6	86.1
M_{th}	-1.06	17.8	18.9	93.3
MARK Model ave	-12.46	28.6	41.1	62.1

4.6. Superpopulation and population estimates

The superpopulation (the population of bears on the sampling grid and surrounding area) was estimated using program CAPTURE models and the Huggins MARK models (Table 9). We conclude that the appropriate estimate for the superpopulation is 133 grizzly bears (SE=18.12, CI=109 to 183) as estimated by the program CAPTURE M_h (Chao) model. Estimates from non-heterogeneity estimators were slightly lower due to heterogeneity variation of capture probabilities. MARK model average estimates were slightly lower than CAPTURE heterogeneity estimators. This could have been due to lower power of MARK to discern and model heterogeneity variation and instability of the recently modified Huggins-Pledger estimator in program MARK (Gary White, Colorado State University, Per. Comm). The estimate of capture probability from the M_h (Chao) was 0.25 which was lower than estimates of capture probability of 0.33 and 0.52 from the 2004 and 2005 DNA inventory projects, respectively. Despite this, levels of precision of estimates was similar to previous years at CV<20%.

Table 9: Superpopulation estimates of grizzly bears for the Alberta grizzly bear management area 5 inventory project. Estimates correspond to bears in the sampling grid and surrounding area. MARK model average estimates correspond to model averaged population estimates from the models listed in Table 7.

Estimator	$\hat{N}$	SE	95% CI		CV
Males and females					
M_{th}	135	22.13	108	199	16.4%
M_h(jackknife)	142	13.34	122	174	9.4%
M_t(Chao)	118	12.82	101	153	10.9%
M_h (Chao)	133	18.12	109	183	13.6%
MARK model ave.	119	23.68	100	162	19.8%
Females					
M_{th}	68	14.07	53	114	20.7%
M_h(jackknife)	70	8.71	58	93	12.4%
M_t(Chao)	59	7.55	50	82	12.8%
M_h (Chao)	66	11.02	53	100	16.7%
MARK model ave.	60	20.02	49	118	33.1%
Males					
M_{th}	68	17.86	49	127	26.3%
M_h(jackknife)	69	9.47	56	94	13.7%
M_t(Chao)	58	9.97	47	89	17.2%
M_h (Chao)	68	15.20	51	115	22.3%
MARK model ave.	60	14.18	49	86	23.5%

4.7. Estimation of average number of bears on the sampling grid and density

The superpopulation estimates were used as the basis for estimates of density in the sampling grid area. Twenty-nine radio collared bears (17 females and 12 males) that occurred on the sampling grid from 1994-2006 had adequate sample sizes of points to allow estimation of closure violation. Using M_h (Chao) for sex-specific population estimates (Table 9), females and males comprised 49% and 51% of the population respectively. We weighted the contribution of each bear in the analysis by the proportion of its sex in the population. This resulted in a weighted mean estimate of 67.6 percent of collared bear locations on the sampling grid. Using this figure, superpopulation estimates were scaled to average population size on the sampling grid (Table 10). This resulted in estimates of average number of bears on the grid at one time of 89.93. Coefficients of variation for average number of bears on the sampling grid were below 20% for the both estimators suggesting adequate precision of average $\hat{N}$ estimates.

Table 10: Superpopulation estimates, proportion of GPS collar locations on sampling grid and the estimated average population size of bears on the sampling grid.

Estimation model	Superpopulation estimate		Proportion GPS bears on grid		Average $\hat{N}$ on sampling grid				
Estimator	$\hat{N}$	S.E.	Estimate	SE	Ave $\hat{N}$	SE	95% CI		CV
M_h (Chao)	133	18.1	67.6%	7.4%	89.93	15.73	75	116	17.5%

The average population size estimates were then divided by grid area (7639 km^2) to obtain density estimates for the 2006 sampling grid area (Table 11).

Table 11: Estimates of density ($\hat{D}$)for the Alberta Unit 5 Inventory area. Density is expressed as bears per 1000 km^2

Estimator	$\hat{D}$	SE	95% Conf. Interval	
M_h (Chao)	11.77	2.06	9.87	15.21

5. Discussion

5.1. Comparison of density with other management units

Population density estimates from the grizzly bear management area 5 inventory in 2006 ($\hat{D}$=11.77, SE=2.06, CI=9.87 to 15.21) were higher than density estimates from the Unit 4 area in 2005 ($\hat{D}$=5.25, SE=0.47, CI=4.87 to 6.09) (Boulanger et al. 2005b) and Unit 3B4B area in 2004 ($\hat{D}$=4.79, SE=0.84, CI=4.10 to 6.28) (Boulanger et al. 2005b).

At this time, the densities between the management units that have been DNA surveyed in the last 3 years (2004, 2005, and 2006) should not be compared. In a naive comparison, one would note the significantly higher densities in 2006 compared to 2004 and 2005 surveys. However, there are several reasons why further analysis is required before these densities can be fairly and accurately compared. First, in 2004 and 2005 we sampled comparatively larger portions of plains and foothills areas where densities of bears are lower. Second, for logistic, financial, and jurisdictional reasons in 2004 and 2005 we did not sample all the way to the Alberta-BC border at the continental divide as we did in 2006 therefore excluding areas that potentially had higher bear densities. In all 3 years, we found a pattern that the grizzly bear DNA capture density was higher in the western portions of the study areas, closer to the continental divide within protected areas. Therefore, differences in estimated densities between grids could be partially due to differences in the proportions of habitat types and protected areas in each of the sampling grids. Our research team is currently working on RSF analyses (Nielsen 2004, Nielsen et al. 2004, Nielsen et al. 2006) that will enable a standardized comparison of habitat-specific densities so managers can have the benefit of comparing population size and density among areas.

5.2. Comparison of mark-recapture results with previous years projects

The estimated capture probability for this project was lower than the two previous years (Table 12). Despite lower capture probabilities, the level of precision for the 2006 estimate was still reasonably high due to the higher number of bears in the population offsetting the effects of lower capture probability variation. Superpopulation estimates were used to compare projects in Table 12 because closure corrected estimates have not been produced for some of these projects. In addition, precision of superpopulation estimates best conveys the precision of the mark-recapture component of a project given that other factors (such as the method used to estimate average number of bears on the grid) will affect the ultimate estimates of density.

Table 12: Superpopulation estimates from DNA mark-recapture projects conducted in British Columbia and Alberta. Projects are ordered by the coefficient of variation of the superpopulation estimate. A lower CV indicates higher estimate precision.

Project	Model	$\hat{N}$	SE	CV	$\hat{P}$	Cell Size(km^2)	Sites moved?	Sessions	Reference[1]
Alberta Unit 4	M_h (Chao)	47	4.79	10.2%	0.52	49	yes	4	(Boulanger et al. 2005a)
Parsnip	M_{th}	386	48.4	12.5%	0.18	64	yes	4	(Mowat et al. 2005)
Alberta Unit 5	***M_h (Chao)***	***133***	***18.12***	***13.6%***	***0.25***	***49***	***yes***	***4***	***(This study)***
Alberta Unit 3	M_h (Chao)	53	8.3	15.7%	0.33	49	yes	4	(Boulanger et al. 2005b)
Jumbo	M_h (Chao)	45	7.1	15.8%	0.26	25	no	4	(Stronen et al. 1999)
Prophet	M_{th}	166	26.2	15.8%	0.17	81	yes	5	(Poole et al. 2001)
UCR 97	M_h (Chao)	55	9.5	17.3%	0.20	25	no	5	(Boulanger et al. 2004)
Kingcome	M_h (Chao)	102	20.7	20.3%	0.19	49	yes	5	(Boulanger and Himmer 2000)
UCR 96	M_h (Chao)	108	23.8	22.0%	0.16	64	yes	4	(Boulanger et al 2004a)
Flathead	M_h (Chao)	156	47.5	30.5%	0.10	64	yes	4	(Boulanger 2001)
UCR 98	M_t (Chao)	92	29.8	32.4%	0.12	25	no	5	(Boulanger et al. 2004)
Granby Kettle	M_t (Chao)	46	16.4	35.7%	0.13	64	yes	5	(Boulanger 2000)

[1]Further details on British Columbia projects can be found in Boulanger et al. (2002)

5.3. Reasons for reduced capture probabilities this year

One of the most probable reasons for reduced capture probabilities in 2006 was that the sampling grid was more open leading to a greater degree of closure violation. Closure violation is evident from the lower estimated proportion of telemetry points on the sampling grid as well as the larger number of bears captured in transect cells on the western border of the sampling grid. Violation of closure leads to reduced capture probability since a proportion of "edge" bears are not vulnerable to sampling during the

entire duration of the project (Boulanger and McLellan 2001), . A comparison of closure (as estimated by the proportion of collared bear locations on the sampling grid) and estimated capture probability for this project and the 2004 and 2005 projects was consistent with this expectation (Figure 5). This result highlights the need for a sampling design that is intensive enough to be robust to various factors that influence captures success and ultimate precision of estimates. For example, if a less intensive sampling design (i.e. larger grid cell size) was used for this project than capture probabilities would have been lower (due to lower sampling intensity and closure violation) which could potentially lead to an imprecise estimate which would be of less utility for bear management. Basically, it is not possible to design grids to be completely closed, therefore other aspects of study design (such as sampling intensity) need to be used to offset the potential detrimental effects of closure violation (such as decreased capture probability).

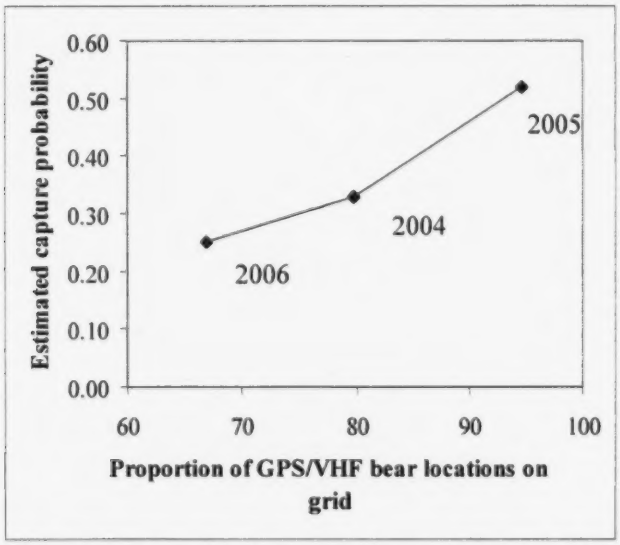

Figure 5: Comparison of capture probability and degree of closure violation as estimated by the proportion of GPS/VHF location on the sampling grid. Data from the 2004, 2005, and 2006 Alberta DNA projects were used for this comparison. Capture probability estimates are from M_h (Chao) as shown in Table 12.

Greater closure violation (Figure 5) in 2006 compared to previous years' grids helps explains why the occupancy probabilities of previously collared bears were lower for the 2006 grid compared to previous years (Figure 4b); because the Unit 5 DNA mark-recapture grid was more open there was less chance that previously collared bears were still on the grid during the time of DNA sampling and this resulted in lower occupancy probabilities. Occupancy probability is analogous to apparent survival in this case. Namely, it estimates the probability that the bear is on the grid. If a bear is not on the

grid then it either died or emigrated from the grid before sampling occurred. One interesting implication of the extensive closure violation across the continental divide is that the Alberta grizzly bear population in this study area is to some level, integrated with the bears in BC. Proctor and Paetkau (2004) demonstrated that the bears across the continental divide south of Hwy 3 in Alberta and British Columbia are acting as 1 interbreeding population.

5.4. Bear distribution in Unit 5 as estimated by DNA sampling

Estimates of population size for Alberta management area 5 assume that the sampling grid sampled, but not necessarily caught, all of the bears in the study area. Transect sites to the east did not capture any bears so it is reasonable to assume that the population size of bears east of the sampling grid was negligible during the time of sampling. As seen in Figure 6, RSF-based habitat values decline substantively beyond the edge of the grid.

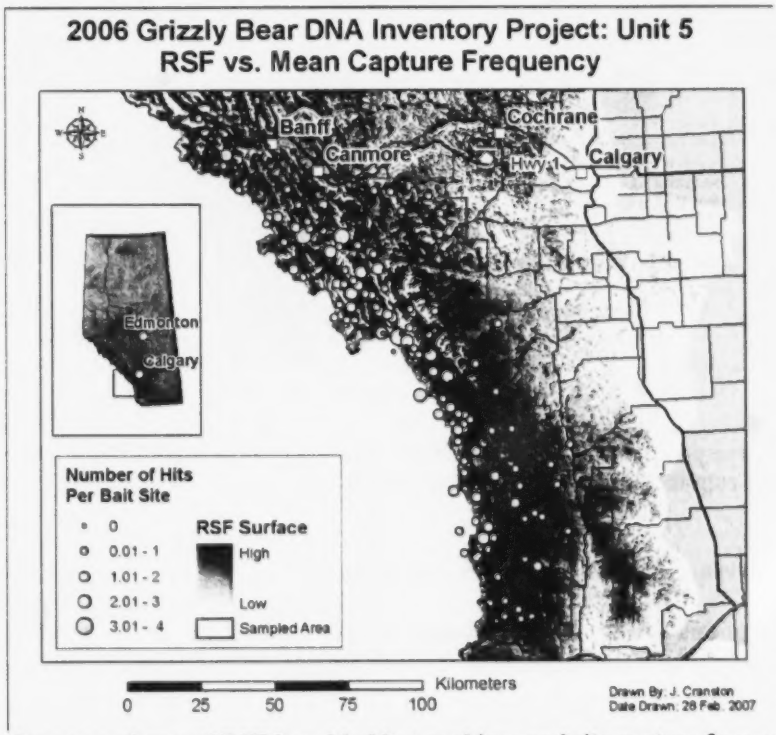

Figure 6: Correspondence of RSF based habitat rankings and site capture frequencies from the 2006 DNA sampling grid.

Another interesting result from this project is the correspondence between distribution of bears (as reflected by the number of hits per hair capture site) and management zones in Alberta (Figure 7). It can be seen that the majority of hits were well within the inhabited

and secure zone. No hits were found in the part of the 'inhabited, secure' zone between the Elbow and Highwood rivers, indicating that this entire zone was not occupied at a high level during the study. We are currently conducting further analysis of the DNA data using occupancy models to gain further understanding of factors influencing distribution.

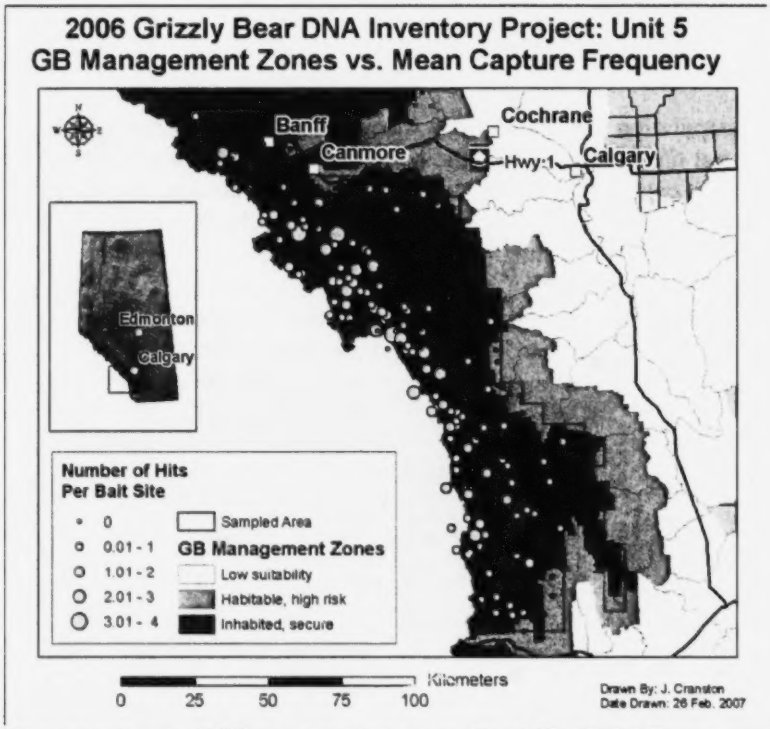

Figure 7: Correspondence of GB management zones (Foothills Model Forest, unpublished data) and site capture frequencies from the 2006 DNA sampling grid.

5.5. Data requirements for future inventory work

The success of this grizzly bear population inventory project was in large part due to the data sets collected for the study area through the Foothills Model Forest Grizzly Bear Research Project over the past 6 years. Having remote sensing based habitat maps, RSF models, and GPS bear movement data proved invaluable in the design and analysis of this DNA population inventory. Figure 6 highlights the general correspondence between RSF habitat scores and the distribution of bears on the sampling grid. This type of information is critical in defining sampling grid boundaries and in the placement of sampling sites.

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8. Appendices

8.1. Appendix 1 : The 2006 DNA mark-recapture sampling grid (Unit 5) in relation to other management units.

8.2. Appendix 2-Details on minimization of bear genotyping errors

Special care was taken to ensure the accuracy of the genetic results. Genetic assignments of individual identity can be compromised if match probabilities are high enough that some individuals will have identical genotypes. It has been demonstrated in several bear populations, using 6-locus marker systems with similar variability to that employed in the current study, that there are stepwise 10-fold decreases in the number of individuals that match at 3 of 6 , 4 of 6 , 5 of 6 , and all 6 markers (Paetkau 2003). We pre-tested the 6-markers that were used in the current study by analyzing 255 samples from hunter-killed bears spanning the north-south range of grizzly bears in Alberta. These 255 genotypes fit the expected pattern with 2276, 255, 19 and 2 pairs of individuals matching at 2, 3, 4 and 5 markers, respectively. As expected from this trend, no pairs of individuals had genotypes that matched at all 6 markers. Given that the number of individuals captured in the current dataset is much smaller (n = 86), and given that we observed 58 and 6 pairs of genotypes in this dataset that matched at 3 and 4 markers, respectively, the probability that we captured even a single pair of individuals with identical genotypes, and thus underestimated the number of captured individuals, is remote. The best estimate of this probability is obtained by taking the number of pairs that match at 4 of 6 markers and

dividing by 100 (Paetkau 2003), and is thus 0.06. In other words, match probabilities were low enough to ensure that each sampled individual had a unique genotype.

The second way that genetic assignments of individual identity can become inaccurate is if errors are incorporated into genotypes, thus causing different samples from the same individual to receive different individual assignments. We followed published recommendations (Paetkau 2003) to demonstrate the reproducibility of each pair of genotypes that were similar enough to have a realistic chance of having originated from genotyping error. Data images showing the replication of the relevant data points are available on request. Note that each individual's genotype differed from that genotype of every other individual at a minimum of 2 markers, and that genotyping error normally creates pairs of genotypes that differ at just 1 marker.

8.3. Appendix 3 : Background information on mark-recapture issues

Several fundamental mark-recapture concepts must be defined to ensure adequate understanding of the concepts discussed in this report.

8.3.1. Definition of a model and estimator

Mark-recapture estimation represents an improvement from traditional count-based census methods. With traditional methods bears would be counted or trapped and the number trapped would be the estimate of population size. Inherent in this is the assumption that all animals have been trapped or counted, otherwise the estimate of population size would be lower than the actual population size. In mark-recapture estimation the percentage of animals captured is estimated. This percentage is called a capture probability. This concept can be expressed by the following formula:

$$\hat{N} = \frac{M}{\hat{p}}$$

In the above formula, M is the census of animals, $\hat{p}$ is the estimate of capture probability, and $\hat{N}$ is the estimate of population size. With traditional census methods $\hat{p}$ is assumed to equal one. An important term can be introduced here. A *model* is a set of assumptions that correspond to an estimation method. In the case of a census, our model is based on the assumption that all animals are caught. Capture probability $\hat{p}$ is rarely equal to one, and, as a result, many models have been formulated that make differing assumptions on how $\hat{p}$ varies. For any model there is a corresponding estimator. An *estimator* is a set of mathematical formulae that allow an estimate using the assumptions of the model. In the case of a count model, the estimate is simply the count of animals caught. The subject of estimation using mark-recapture methods has seen much theoretical attention, and, therefore, many estimators exist which are much more complex than simple counts.

8.3.2. Bias, precision and robustness

Estimates of density and population size are evaluated using two principle measures: precision and bias. The best way to conceptualize precision and bias is to consider what a range of estimates might look like if a project was repeated many times (Figure 8).

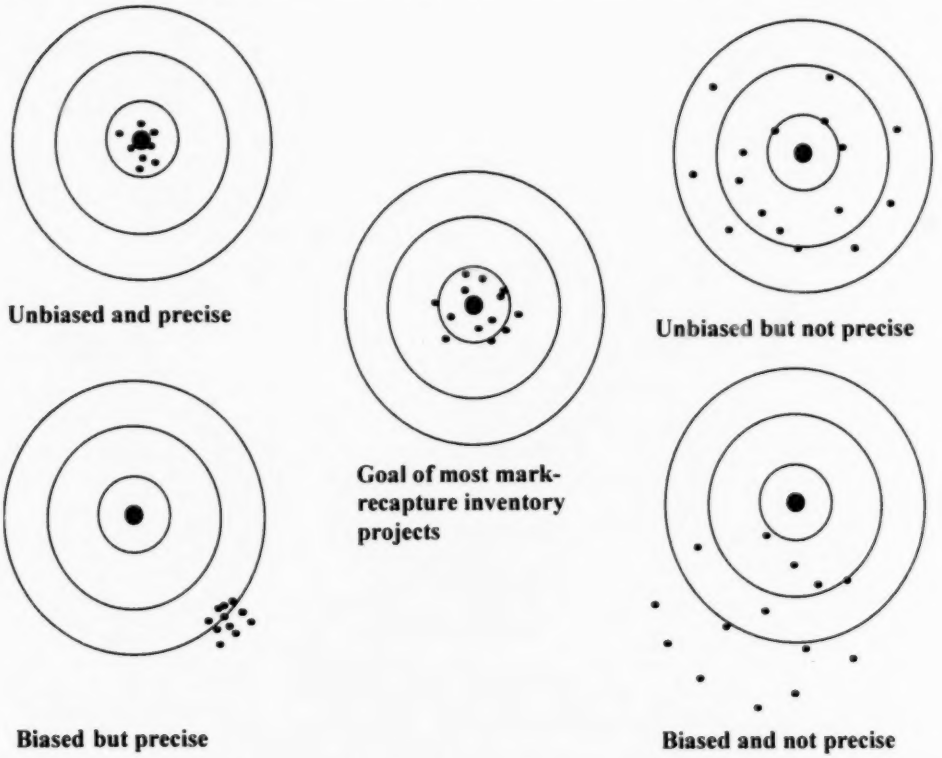
Unbiased and precise
Unbiased but not precise
Goal of most mark-recapture inventory projects
Biased but precise
Biased and not precise

Figure 8: A conceptual diagram of bias and precision. Each target represents a possible set of estimates ("shots") from the mark-recapture experiment, if the study were repeated many times. Lack of precision is mainly caused by low sample sizes, and bias is caused by improper model selection. Unlike this target analogy, most mark-recapture experiments are only conducted once (i.e. one "shot") and the true bulls eye (true population size) is not known. Therefore, mark-recapture data should be interpreted cautiously and statistically to avoid erroneous conclusions (target figure from White et al. 1982).

Precision is the repeatability of estimates and is usually estimated by the coefficient of variation and the width of confidence intervals. *Bias* is the deviation of estimates from the true population value and is determined by how well the statistical model and estimator fit the mark-recapture data. The goal of most mark-recapture experiments is to minimize bias and maximize precision therefore minimizing potential error in estimates.

An ideal estimator of population size or density should be unbiased, precise, and robust. *Robustness* is a measure of how well an estimator will perform even when its associated assumptions about capture probability are violated. An example of a robust estimator would be one that assumes equal capture probabilities but still gives unbiased estimates when moderate capture probability variation exists in the data.

8.3.3. Key issues in optimal inventory design

Proper sampling design is critical to obtaining reliable population estimates. The following is a list of the three main issues in the design of projects to estimate population size (White et al. 1982).

1. *Meeting the assumption of geographic and demographic closure*: If closed population estimation models are used, then it is assumed that the population is closed or "no animals leave, enter, die or are born during the sampling process." Violation of closure can cause substantial biases in estimates from most mark-recapture models. If closure violation is occurring, mark-recapture population estimates will pertain to the "superpopulation" of bears in the *sampling grid and surrounding area during the time that sampling was conducted.* (White 1996, Kendall 1999). For estimation of density and comparison of different areas the average number of bears on the sampling grid is most applicable. Radio collared bears or the methods of Boulanger and McLellan (2001) can be used to account for closure violation.
2. *Sample size*: Sample size is determined by the number of animals in the trapping area, the capture probability of the population, and the number of times the population is sampled. In general, higher population capture probabilities are needed for smaller population sizes to obtain adequate estimates. The primary effect of low sample size is reduced estimate precision. In addition, if sample size is low, then not enough data will be available to determine dominant capture probability variation in the data set leading to erroneous model selection.
3. *Capture probability variation*: Bears probably show unequal probabilities of capture which can lead to biased population estimates. It is possible to test data to determine the dominant type of capture probability variation, if the above issues are met. Capture probability variation can be divided into three categories.

a) Heterogeneity: Each animal has a unique probability of capture that is constant throughout the study.

b) Behaviour: All animals have an equal initial capture probability but this changes after initial capture.

c) Time: The capture probability of bears changes evenly each time sampling occurs.

Program CAPTURE and MARK have estimation models that are formulated to accommodate each form of capture probability variation. The models (and corresponding capture probability assumptions) are M_o (null or equal capture probabilities), M_h (heterogeneity), M_t(time), M_b(behaviour), M_{th} (time/heterogeneity), M_{bh}(behaviour/heterogeneity), M_{tb}(time/behaviour) and M_{tbh}(time/behaviour/heterogeneity).

If the goals of study design are met, the most appropriate estimation model can be used for population estimates, which should yield the most precise and unbiased results. Conversely, if an inventory is designed poorly, a complex, imprecise model may have to be used (to minimize bias), or, if assumption violations are severe, *no estimator* will give a reliable estimate (Otis et al. 1978).

8.4. Appendix 4: Details about simulation methods

8.4.1. Expert opinion simulations

One of the most likely forms of capture probability variation in grizzly bear data sets is heterogeneity variation due to females and cubs displaying reduced capture probabilities. Unfortunately, age cannot be determined from DNA therefore this a non-identifiable form of heterogeneity. This form of heterogeneity is difficult to detect given the lower power of model selection routines with sample sizes typical of bear populations (Boulanger et al. 2002). The problem of low cub capture probabilities is especially relevant to the current design of most DNA mark-recapture projects that use a single strand of barbed wire that cubs may be able to go under without getting snagged (Boulanger et al. 2004)

Boulanger et al. (2004) used data from known female bear with cubs monitored during DNA sampling to estimate the probability of capture of cubs. In addition, they hypothesized capture probabilities of other age classes of bears based on their height relative to hair snag wire. Parameters used for simulations are presented in Table 13. Proportions of each age and sex class ($P_{age\text{-}sex}$) are from McLellan (1989). P_{snag} the proportion of each cohort snagged relative to adult males, was hypothesized upon bear height relative to barb wire and trap encounter rates for yearlings and females. P_{cohort} was the capture probability of each age and sex cohort. P_{cohort} was the product of P_{snag} and P_{cohort} for adult males. For cubs, P_{cohort} was also estimated from 7 cubs and their 4 radio collared mothers that were tracked during the Upper Columbia River 1996 DNA mark-recapture project. The mean capture probability for simulations ($\bar{p}$) was estimated as

$\sum_{j=1}^{4} P_{age-sex} p_{cohort}$ where j is a given age and sex class. Male capture probability (p_{cohort}) was varied to meet the desired mean capture probability level for a simulation.

Table 13: An example of heterogeneity simulation parameters. Proportions of age class ($P_{age-sex}$), expected number of bears (E(N)), proportion of age class snagged (p_{snag}), capture probability (p_{cohort}).

Age	Sex	$P_{age-sex}$	p_{snag}	p_{cohort}
Cub	males and females	0.215	0.24	0.17
Yearlings	males and females	0.175	0.75	0.53
Adult	females	0.305	0.75	0.53
Adult	males	0.305	1.00	0.70

One set of simulations was conducted with heterogeneity variation parameterized in Table 14. Another set of simulations was conducted with time and heterogeneity variation. The level of time variation was directly estimated from the Alberta 2006 study (Table 14). Time variation was standardized so that it would vary so that the mean capture probability level from any simulation was constant. This was done by first estimating capture probability for each sample session $\hat{p}_j$ as:

$$\hat{p}_j = {}^{n_j}\!/_{\hat{N}}$$

where n_j is the number of bears captured for session j and $\hat{N}$ is the population size estimate. The average capture probability $\bar{p}$ was then estimated by the sum of individual capture probabilities divided by the number of sessions. A capture probability "multiplier" was then estimated by

$$mult_j = {}^{\hat{p}_j}\!/_{\bar{p}}$$

The capture probabilities for any cohort in Table 13 for a given session were therefore equal to its individual capture probability times the multiplier for that session. Using this approach ensured that the mean population capture probability level did not change even when time variation was simulated. This is the same approach used in the simulation module in program CAPTURE (Otis et al. 1978).

Table 14: Time parameterization for simulations based upon animals caught in Alberta 2006 DNA mark-recapture project.

Statistic	j=1	2	3	4
Animals caught n_j	30	30	40	34
$\hat{p}_j$ for period j	0.24	0.24	0.32	0.27
multiplier for $\bar{p}$	0.90	0.90	1.19	1.02

8.4.2. Data-based simulations

A set of simulations was conducted based on levels of heterogeneity and time variation estimated directly from mark-recapture data. For this analysis, levels of heterogeneity were estimated by mixture models. Mixture models use a mixture of ≥2 capture probabilities to model heterogeneity of a single capture probability (Pledger 2000). This allows bimodal or multimodal distributions that may arise from heterogeneity of capture probabilities to be modeled. For example, the overall capture probability for an encounter history where a mixture of A distributions is used is $\sum_{i=1}^{A} \pi_i \theta_i^v (1-\theta_i)^{t-v}$, where v equals the number of captures of the animal for t occasions, π_i is the probability the animal has capture probability θ_i, with the sum of the π_i forced to equal 1. Thus, for A = 2, $\pi_2 = 1-\pi_1$. Different values of capture probabilities were simulated for each mixture distribution for models in Table 7.